WOOD AND BARK ANATOMY OF *TAKHTAJANIA* (WINTERACEAE); PHYLOGENETIC AND ECOLOGICAL IMPLICATIONS[1]

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ABSTRACT

Wood and bark anatomy of *Takhtajania* are newly reported on the basis of woody stems to 4.5 cm in diameter, a woody root 4 cm in diameter, and a smaller stem with only a little secondary growth. The wood lacks growth rings and is vesselless. Tracheids bear biseriate or triseriate circular pits or scalariform pits on end walls and sparse circular pits on side walls. Warts and helical thickenings are lacking on the inner surfaces of tracheids. Axial parenchyma is very sparse. Multiseriate and uniseriate rays are about equally abundant, and both are composed of upright cells except for a small number of procumbent cells in multiseriate rays. Ethereal oil cells and sclereids are absent in rays. Bark contains sclereid nests and ethereal oil cells. Wood features closely match those of *Tasmannia* or *Drimys*, in agreement with conclusions reached on the basis of molecular data. Comparative data on bark of Winteraceae other than *Takhtajania* are lacking. Wood features of *Takhtajania* agree with those of subtropical species by lacking features found in temperate Winteraceae (growth rings, warted tracheid surfaces, helical thickenings in tracheids).

Key words: ecological wood anatomy, Magnoliidae, *Takhtajania*, tracheids, vessellessness, Winteraceae.

Wood of Winteraceae has been surveyed at the species level for all genera except *Takhtajania*. The herbarium specimen of *Takhtajania* hitherto available did not have sufficient secondary xylem for satisfactory study; twigs are often of limited value in determining the nature of wood anatomy of a species. Rediscovery of *Takhtajania* has been described in an accompanying paper of this series (Schatz, 2000 this issue).

Winteraceae have traditionally been regarded as retaining numerous character states primitive for dicotyledons (e.g., Dahlgren, 1975; Takhtajan, 1987; Thorne, 1992). Recent molecular studies (e.g., Qiu et al., 1993) place Magnoliales, which contain Winteraceae, at a low level of advancement, but place other orders of flowering plants (notably paleoherbs) as basal to Magnoliales. A primitive status among dicotyledons for paleoherbs has been advanced by Taylor and Hickey (1992). Wood of *Takhtajania* is of potential interest in assessing the position of Winteraceae. The position of *Takhtajania* within Winteraceae can be assessed on the basis of wood anatomy, because wood character states within the family are sufficiently diverse that a key could be constructed on the basis of wood data alone (Carlquist, 1989).

Another phylogenetic question regarding Winteraceae has been raised by the assertion (e.g., Young, 1981) that woody groups of vesselless dicotyledons (Amborellaceae, Tetracentraceae, Trochodendraceae, Winteraceae) may be secondarily vesselless rather than primarily so. The latter view (e.g., Bailey, 1944) has been widely propagated.

Ecological questions also are of significance. The presence of growth rings, warted inner wall surfaces of tracheids, and helical thickenings in secondary xylem tracheids characterize more temperate species of *Drimys* (Carlquist, 1988a), *Pseudowintera* (Patel, 1974; Meylan & Butterfield, 1978), and *Tasmannia* (Carlquist, 1989). These features are lacking in species that occupy subtropical or frost-free sites, as shown by *Belliolum* (Carlquist, 1983a), *Bubbia* (Carlquist, 1983b), *Exospermum* (Carlquist, 1982a), and *Zygogynum* (Carlquist, 1981). The ecology of *Takhtajania*, which grows along a moist ridge in montane tropical Madagascar, has been described in an accompanying paper (Feild et al., 2000 this issue).

Information is offered on bark anatomy of *Takhtajania* here. This information may serve for comparison when studies of bark anatomy, currently lacking (Metcalfe, 1987), are offered.

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MATERIALS AND METHODS

The first collection of *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy made available to me is documented by the collection *Pierre Jules Rakotomalaza et al. 1342* (MO). The collection locality is in the Anjanaharibe-Sud Special Reserve southwest of Andapa in northeastern Madagascar (Schatz, 2000), along a ridge in which many of the *Takhtajania* trees are semi-prostrate and covered with lichens. This collection provided liquid-preserved material of a woody stem 3.5 cm in diameter and a portion of a stem with only a little secondary growth. A second collection from this locality, *Chris Birkinshaw 483* (MO), provided a liquid-preserved stem 4.5 cm in diameter and a root 4 cm in diameter. All of these materials were originally preserved in formalin-acetic alcohol and were transferred to 50% aqueous ethanol.

Sections of the smaller stem and the larger stems and the root (all with both bark and wood) were prepared according to the schedule of Carlquist (1982b). In addition, sections of the stem 3.5 cm in diameter, the stem 4.5 cm in diameter, and the root 4 cm in diameter were prepared on a sliding microtome. Some of these sections were dried between glass slides, sputter-coated, and examined with scanning electron microscopy (SEM). Other sliding microtome sections were stained with a safranin-fast green combination and mounted in Canada balsam. Macerations of the wood of the larger stems and of the root were prepared with Jeffrey's Fluid and stained with safranin. Mean tracheid diameter is based upon tangential diameter of tracheids. Thickness of radial walls is used for measurements of wall thickness. Means are based on 25 measurements except for tracheid wall thickness, in which wall portions judged to be typical were used.

ANATOMICAL RESULTS

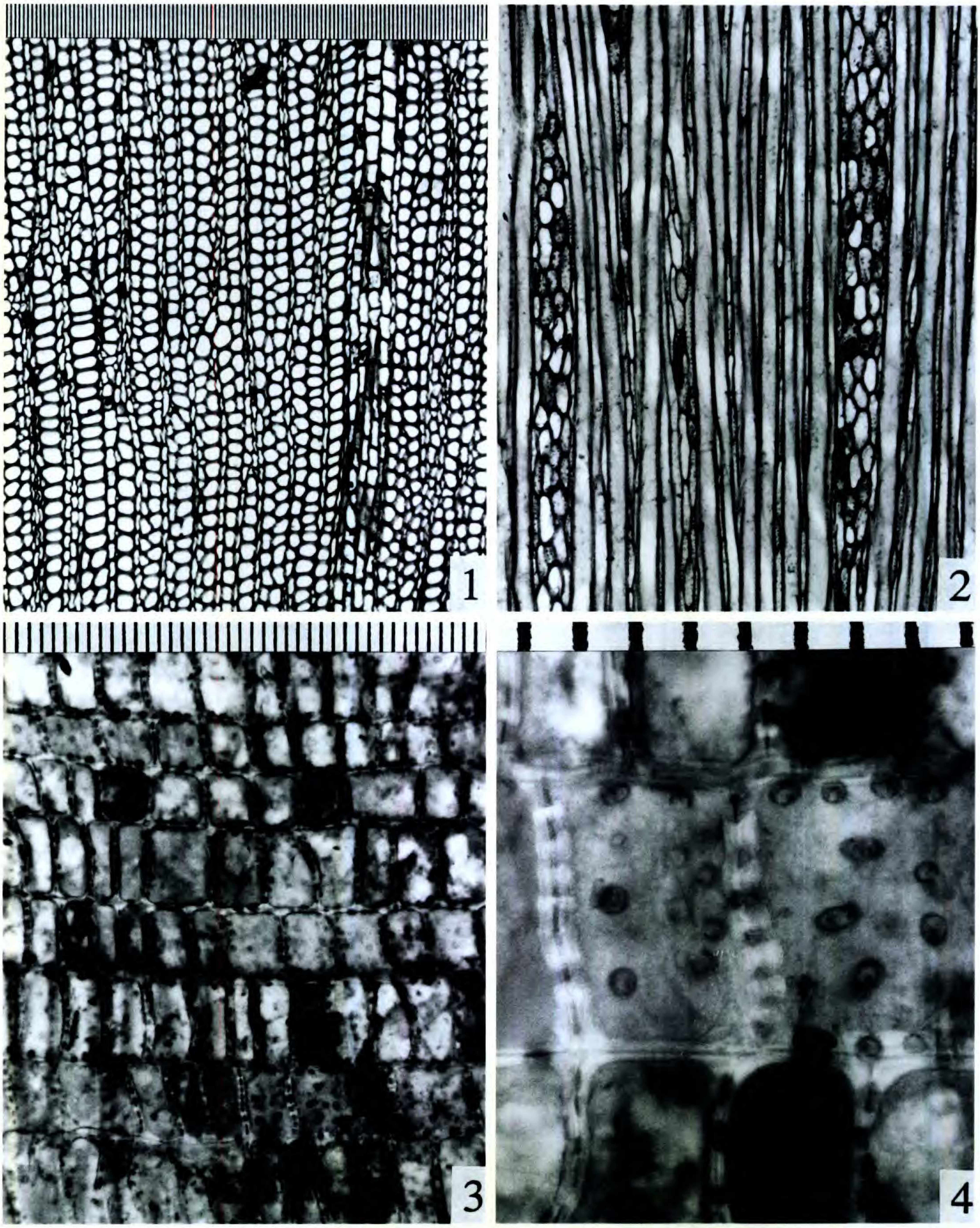
WOOD (FIGS. 1–9)

Data are based on mature wood of the stem 3.5 cm in diameter unless otherwise indicated. Quantitative data for the two large stems were not considered significantly different from those of the large root (except for tracheid length), so only data on the stem 3.5 cm in diameter form the basis for the description below.

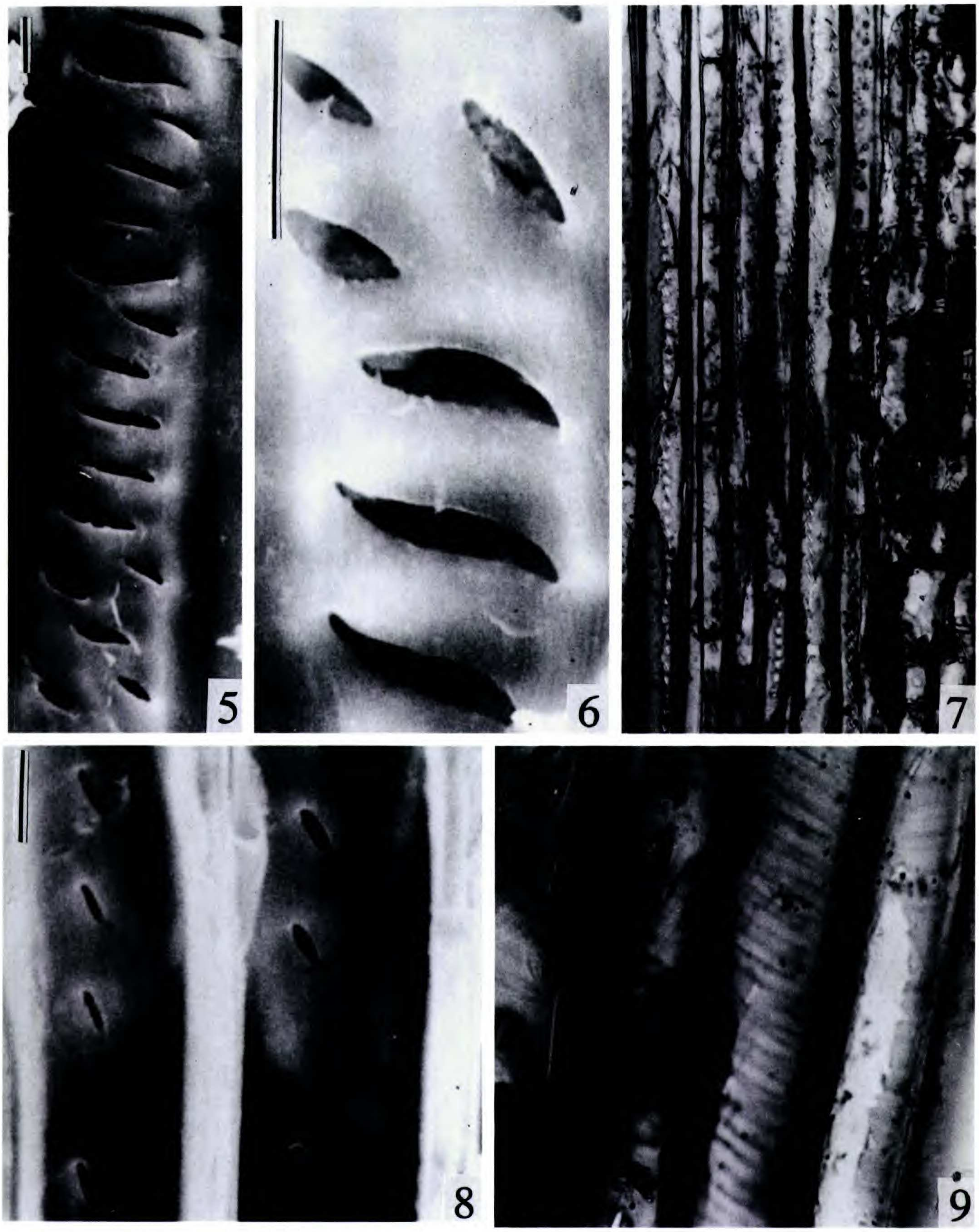
Growth rings absent (Fig. 1). Tracheary elements all tracheids (Figs. 1, 2, 5–9). Mean tracheid length (largest stem), 3002 μm. Mean tracheid length (root), 3821 μm. Mean tracheid lumen diameter, 38 μm. Mean tracheid wall thickness, 4.3 μm. Lateral walls of tracheids with scattered circular bordered pits (Figs. 7, 8). End walls of tracheids with biseriate circular bordered pits or scalariform pits (Figs. 5, 6), the latter sometimes more crowded than shown in Figure 5. Pit membranes present in end wall pits (Fig. 6), both in stems and in root. Tracheids with scalariform pits less common than those with circular pits on end walls formed in small groups with no apparent pattern of distribution within the wood. Tracheids with scalariform end-wall pitting somewhat more common in the root studied than in the stems. Circular pits with narrowly elliptical apertures (Figs. 8, 9), pit cavities about 9 μm in diameter as seen in face view. A small number of tracheids with characteristic elongate elliptical thin areas oriented transversely to helically on inner wall surfaces; these are not like helical thickenings reported in *Pseudowintera* and one species of *Tasmannia* (Carlquist, 1989). Warts absent on tracheid wall inner surfaces (Figs. 5, 8). Pitting generally more abundant on radially oriented walls, but end-wall pitting may be seen on radially oriented and diagonally oriented tracheid walls. Axial parenchyma very scarce (Fig. 7, left), distributed in a diffuse fashion and composed of strands of five or six cells. Rays multiseriate and uniseriate (Fig. 2), about equally frequent (if biseriate rays are included among multiseriate rays). Multiseriate rays are more common than the photograph of Figure 2 suggests because there are long uniseriate wings on most multiseriate rays. Multiseriate rays up to five cells in width at widest point (Fig. 2), mean multiseriate ray width 2.5 cells. Mean multiseriate ray height, 4176 μm; mean uniseriate ray height 1473 μm. Uniseriate rays composed of erect cells; multiseriate rays composed mostly of square to erect cells, a few procumbent cells present (Fig. 3), and the ray type of the species thus intermediate between Heterogeneous I and Paedomorphic I (Carlquist, 1988b: 179). Ray cells with thick lignified walls, most pits bordered as seen either in sectional (Fig. 4) or face view. Borders well developed on pits of tangentially oriented ray cell walls. Some ray cells with dense, granular, dark-staining contents interpreted here as tannins (Figs. 3, 4). Ethereal oil cells and sclereids absent in rays. Wood nonstoried.

BARK

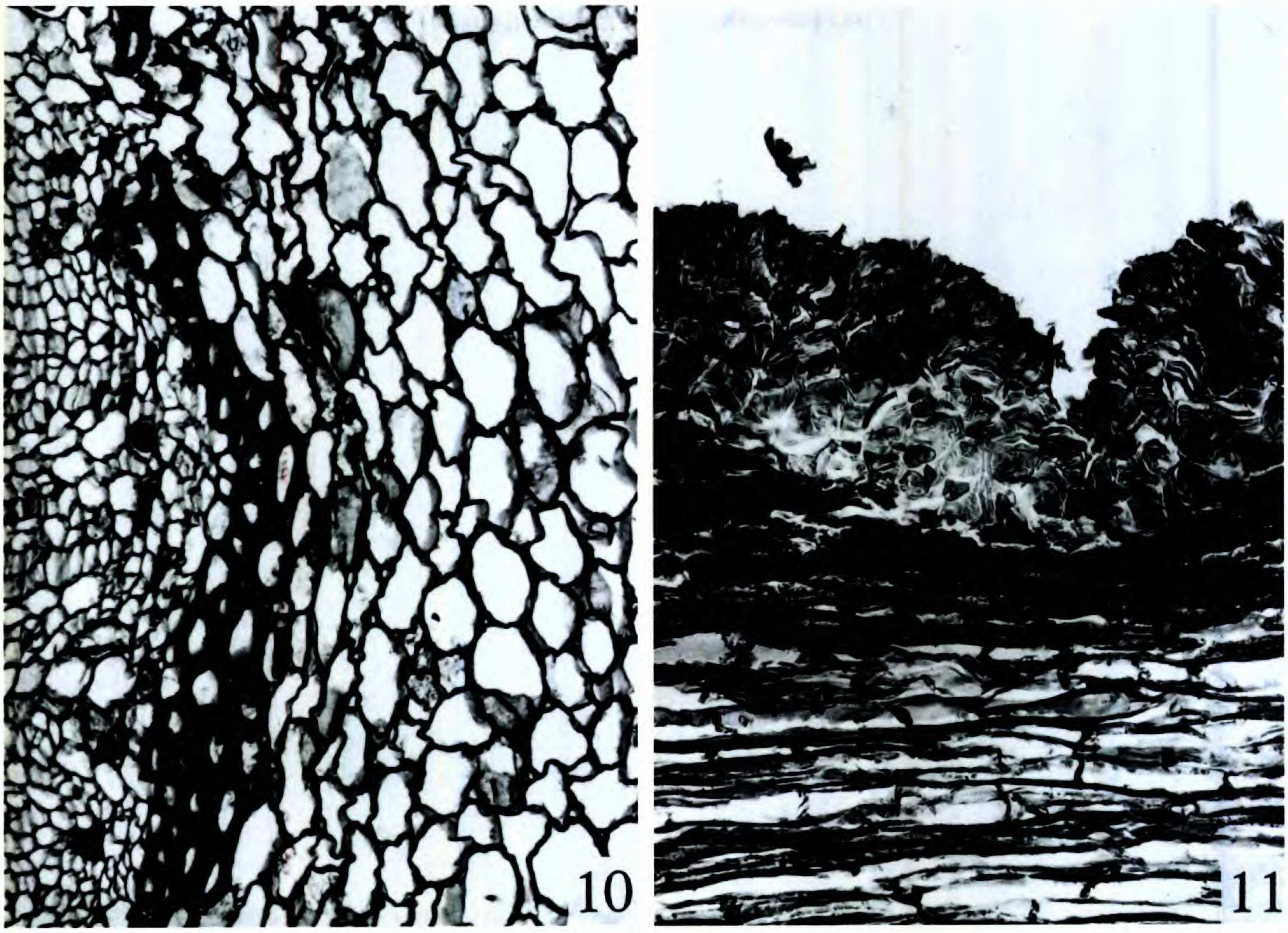
At the periphery of the phloem, a sheath of fibers develops (Fig. 10). These can be termed protophloem fibers. Fibers were not observed within the secondary phloem. In bark of the larger specimens, nests of thick-walled brachysclereids (not illustrat-



Figures 1–4. Sections of wood of *Takhtajania perrieri.* —1. Transection, showing vesselless nature and lack of growth rings. —2. Tangential section; both multiseriate and uniseriate rays are present. —3. Radial section; most ray cells are upright; a few square and procumbent cells are near top of photograph. —4. Portion of ray cells from radial section, showing bordered pits in sectional view and dark-staining contents. Figs. 1, 2, magnification scale above Fig. 1 (divisions = 10 μm); Fig. 3, scale above Fig. 3 (divisions = 10 μm); Fig. 4, scale above Fig. 4 (divisions = 10 μm).



Figures 5–9. SEM photographs (5, 6, 8) and light microscope photographs (7, 9) of wood sections of *Takhtajania perrieri*. —5. End wall of tracheid from radial section, showing both scalariform and circular pits. —6. Scalariform and oval pits from end wall of tracheid of radial section, to show presence of pit membranes, which have been fractured because of handling or preservation method. —7. Radial section, with ray cells at right and a strand of axial parenchyma at left. —8. Inside surface of two tracheids from radial section; walls are smooth. —9. Tracheids from radial section; sparse circular pits in tracheids at left; tracheid to right of center has laterally elongate elliptical thin areas. Figs. 5, 6, 8, magnification scales at upper left (bars = 10 μm). Fig. 7, scale above Fig. 3; Fig. 9, scale above Fig. 4.



Figures 10, 11. Transections of bark of *Takhtajania perrieri.* —10. Section from younger stem, with phloem at left, cortex at right, to show sheath of protophloem fibers (dark). —11. Section from older stem, to show tangentially stretched cortical cells (below) and phellem (above); lamellate walls may be seen in some phellem cells. Figs. 10, 11, magnification scale above Figure 3.

ed here) are present in bark tissue that represents tangentially stretched cortical cells. Scattered ethereal oil cells are also present in this bark tissue.

Phellem is notably thick on the older stems studied (Fig. 11). As seen at higher magnifications, the walls of the phellem cells are clearly lamellate.

ECOLOGICAL CONCLUSIONS

Presence of growth rings, presence of warts on inner walls of tracheids, presence of helical thickenings in tracheids, and to a certain extent, narrowness of tracheids have been interpreted as related to coldness in habitats of particular species of Winteraceae (Carlquist, 1989, and papers cited therein). *Takhtajania* lacks all of these features. From this evidence alone, one could conclude that *Takhtajania* grows in a frost-free zone, in contrast to the habitats of, for example, *Pseudowintera.*

Length of vessel elements is related to ecology in vessel-bearing dicotyledons (Carlquist, 1975). In vesselless angiosperms, as in vesselless gymnosperms, tracheid length is primarily related to diameter of axis from which a wood sample was taken (Carlquist, 1975: 141). The tracheid length recorded here for *Takhtajania* is consonant with that concept, because the sample was taken from a relatively small tree. The greater length of tracheids in the root as compared to those of the stem is in accordance with data by Patel (1965) that root vessel elements are longer than stem vessel elements in dicotyledons at large. Sections and macerations suggested that scalariform end-wall pitting on roots was somewhat more abundant in tracheids of roots as compared to those of stems.

PHYLOGENETIC CONCLUSIONS

In the summary of woods of Winteraceae (Carlquist, 1989), a key based on wood of the genera other than *Takhtajania* was presented. Now that *Takhtajania* wood has become available, one can place this genus in the key. *Takhtajania* falls closest to *Tasmannia.* In both genera, scalariform pitting appears in some tracheids (at least in the earlier years of secondary xylem formation), multiseriate rays average between 2.1 and 4.1 cells at widest point, procumbent cells are scarce in multiseriate rays, and ethereal oil cells are absent in rays. The wood of *Drimys* is similar, differing in having more abundant procumbent cells in rays. These results are interesting in that the molecular data now at hand (Karol et al., 2000 this issue) show greater similarity between *Takhtajania* and *Tasmannia* or *Drimys* than between *Takhtajania* and either *Belliolum, Bubbia, Exospermum, Pseudowintera,* or *Zygogynum.* In view of the fact that molecular results (Karol et al., 2000) show *Takhtajania* to be basal within Winteraceae, wood features of *Takhtajania,* as well as those of *Drimys* and *Tasmannia,* can be expected to exhibit more numerous primitive character states than those of the other genera.

Bark anatomy of *Takhtajania* cannot be compared to bark of other Winteraceae because few data have been accumulated on bark anatomy in the family (Metcalfe, 1987). Esau and Cheadle (1984) have described secondary phloem of Winteraceae in detail, but were not concerned with broader aspects of bark in the family.

Literature Cited

Bailey, I. W. 1944. The development of vessels in angiosperms and its significance in morphological research. Amer. J. Bot. 311: 421–428.

Carlquist, S. 1975. Ecological Strategies of Xylem Evolution. Univ. California Press, Berkeley and Los Angeles.

———. 1981. Wood anatomy of *Zygogynum* (Winteraceae); Field observations. Bull. Mus. Natl. Hist. Nat. Paris, B, Adansonia, sér. 4, 8: 281–292.

———. 1982a. *Exospermum stipitatum* (Winteraceae): Observations on wood, leaves, flowers, pollen, and fruit. Aliso 10: 277–289.

———. 1982b. The use of ethylene diamine in softening hard plant structures for paraffin sectioning. Stain Technol. 57: 311–317.

———. 1983a. Wood anatomy of *Belliolum* (Winteraceae) and a note on flowering. J. Arnold Arbor. 64: 161–169.

———. 1983b. Wood anatomy of *Bubbia* (Winteraceae), with comments on origin of vessels in dicotyledons. Amer. J. Bot. 70: 578–590.

———. 1988a. Wood anatomy of *Drimys* s. s. (Winteraceae). Aliso 12: 81–95.

———. 1988b. Comparative Wood Anatomy. Springer-Verlag, Berlin and Heidelberg.

———. 1989. Wood anatomy of *Tasmannia*; Summary of wood anatomy of Winteraceae. Aliso 12: 257–275.

Dahlgren, R. M. T. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. Bot. Not. 128: 119–147.

Esau, K. & V. I. Cheadle. 1984. Anatomy of the secondary phloem in Winteraceae. I. A. W. A. Bull., N.S. 5: 13–43.

Feild, T. S., M. A. Zwieniecki & N. M. Holbrook. 2000. Winteraceae evolution: An ecophysiological perspective. Ann. Missouri Bot. Gard. 87: 323–334.

Karol, K. G., Y. Suh, G. E. Schatz & E. A. Zimmer. 2000. Molecular evidence for the phylogenetic position of *Takhtajania* in the Winteraceae: Inference from nuclear ribosomal and chloroplast gene spacer sequences. Ann. Missouri Bot. Gard. 87: 414–432.

Metcalfe, C. R. 1987. Anatomy of Dicotyledons, Ed. 2, Vol. 3. Magnoliales, Illiciales, and Laurales. Clarendon Press, Oxford.

Meylan, B. A. & B. G. Butterfield. 1978. The structure of New Zealand woods. D. S. I. R. Bull. 222: 1–250. Wellington, New Zealand.

Patel, R. N. 1965. A comparison of the anatomy of the secondary xylem in roots and stems. Holzforschung 19: 72–79.

———. 1974. Wood anatomy of the dicotyledons indigenous to New Zealand. 4. Winteraceae. New Zealand J. Bot. 11: 587–598.

Qiu, Y.-L., M. W. Chase, D. H. Les & C. R. Parks. 1993. Molecular phylogenetics of the Magnoliidae: Cladistic analyses of nucleotide sequences of the plastid gene *rbc*L. Ann. Missouri Bot. Gard. 80: 587–606.

Schatz, G. E. 2000. The rediscovery of a Malagasy endemic: *Takhtajania perrieri* Winteraceae. Ann. Missouri Bot. Gard. 87: 297–302.

Takhtajan, A. 1987. Systema Magnoliophytorum. Oficina Editoria "NAUKA," St. Petersburg.

Taylor, D. W. & L. J. Hickey. 1992. Phylogenetic evidence for the herbaceous origin of angiosperms. Pl. Syst. Evol. 180: 137–156.

Thorne, R. F. 1992. Classification and geography of the flowering plants. Bot. Rev. 58: 225–348.

Young, D. A. 1981. Are the angiosperms primitively vesselless? Syst. Bot. 6: 313–330.